Annals of Applied Biology ISSN 0003-4746

RESEARCH ARTICLE

Estimation of genetic variability and heritability for biofuel feedstock yield in several populations of switchgrass

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Keywords
Biomass yield; genetic gain; heritability; progeny–parent regression; switchgrass.

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Received: 17 June 2007; revised version accepted: 2 August 2007.

doi:10.1111/j.1744-7348.2007.00186.x

Abstract

Information on heritability and predicted gains from selection for increased biomass yield for ethanol production in switchgrass is limited and may vary among breeding populations. The purpose of this study was to estimate heritability and predicted gains from selection for higher biomass yield within a lowland ecotype switchgrass population, Southern Lowland 93 (SL-93), and two upland ecotype switchgrass populations, Southern Upland Northern Upland Early Maturing (SNU-EM) and Southern Upland Northern Upland Late Maturing (SNU-LM). Narrow-sense heritabilities (h_n^2) for biomass yield in each of the three populations were estimated via progeny–parent regression analysis. Half-sib (HS) progeny families from 130 randomly selected plants from the SL-93 population were evaluated for biomass yield in replicated trials in 2002 and 2003. Clonal parent plants were evaluated for biomass yield in separate environments to provide unbiased h_n^2 estimates from progeny–parent regression. Yield differences were highly significant among SL-93 HS progenies within and over years. For the SL-93 population, h_n^2 estimates were 0.13 and 0.12 based on individual plant and phenotypic family mean (PFM) selection, respectively. Predicted genetic gains (ΔG) per selection cycle were 0.15 kg dry matter (dm) plant^{-1} and 0.10 kg dm plant^{-1} for PFM and individual plant selection methods, respectively. For the SNU-EM and SNU-LM populations, year and year × HS family effects were highly significant ($P < 0.01$) and the HS family effect over years was non-significant ($P < 0.05$). However, HS family effects were highly significant within respective years ($P < 0.01$). Estimates of h_n^2 for the SNU-EM and SNU-LM populations based on PFM and individual plant selection were similar, ranging from 0.44 to 0.47; ΔG per selection cycle ranged from 0.22 to 0.33 kg dm plant^{-1}. The magnitudes of the estimates of additive genetic variation suggest that selection for higher biomass yield should be possible. The substantial effect of environment on biomass yields in the upland populations and the failure of families to respond similarly over years stress the importance of adequately testing biomass yield over years.

Introduction

Switchgrass (*Panicum virgatum*, L.) is a C_4, perennial, determinate bunchgrass, indigenous to the tall grass prairies east of the Rocky Mountains (Sanderson, 1992; Hopkins *et al.*, 1995).

Two major ecotypes, lowland and upland, have been recognised based on morphology and edaphic conditions

(Porter, 1966). Plants of lowland ecotypes are typically more robust, exhibiting stems that are more coarse and thicker in diameter than their upland counterparts. Plants of upland ecotypes are generally shorter and finer with respect to stem and leaf characters and are better adapted to drier habitats, droughty conditions and marginal soils than their lowland counterparts. Extensive variation exists within each of these two major ecotypes for a number of traits of interest.

Switchgrass has two cytotypes, L and U, that are associated with the lowland and upland ecotypes, respectively (Martinèz-Reyna *et al.*, 2001). Switchgrass is allogamous and polymorphic with reported chromosome numbers ranging from $2n = 2x = 18$ to $2n = 12x = 108$ (Nielson, 1944; Henry & Taylor, 1989). Cross-pollination in the species is enforced by a gametophytic self-incompatibility system that is similar to the S-Z incompatibility system found in other Poaceae (Talbert *et al.*, 1983; Martinèz-Reyna & Vogel, 2002; Taliaferro, 2002). All confirmed lowland ecotypes have been tetraploids ($2n = 4x = 36$) and most upland ecotypes are octoploids ($2n = 8x = 72$) (Hopkins *et al.*, 1996).

Traditionally, switchgrass is used in pasture and rangeland plantings as a monoculture and in mixed plantings with other grasses and in conservation plantings (Moser & Vogel, 1995). However, in the past decade, switchgrass has been a focus for input in biofuel production. Switchgrass has been bred primarily to enhance its nutritional value as a forage crop (Vogel *et al.*, 1989). Hence, switchgrass has been managed primarily for high leaf-to-stem ratio and nutrient content via multiple cuttings throughout the growing season (McLaughlin *et al.*, 1999). However, these targets are somewhat divergent for the targets of biofuel crops for which high cellulose content optimised with high biomass production is a primary concern (McLaughlin *et al.*, 1999). Research conducted at Auburn University in Alabama indicated no significant yield differences between one- and two-cut systems for switchgrass harvest but noted that later harvests (one cut) produced a lower ash content (McLaughlin *et al.*, 1999). Studies of switchgrass harvest methods at Virginia Tech University indicated that a two-cut system would produce significantly greater yield than a one-cut system, but the study concluded that economic gains from the two-cut system probably would not offset increased harvest costs (Sanderson *et al.*, 1996). Several studies have shown that a single harvest of switchgrass ranging from late fall to early winter results in the highest sustainable biomass yields coupled with good stand persistence from year to year (Parrish & Fike, 2005). Hopkins *et al.* (1995) reported that switchgrass digestibility for cattle decreases with later harvests, supporting the notion that optimal harvest times for switchgrass for forage and biofuel production are not congruent. Moreover, Sanderson *et al.* (1999) reported that forage quality decreased with age of switchgrass biomass regrowth, while total yields decreased as harvest frequencies increased.

Over the past decade, switchgrass has been the focus of a multi-institutional, collaborative research effort to develop it as a herbaceous energy crop (HEC). The potential of switchgrass as an HEC derives mainly from its broad geographic adaptation, ability to grow on marginal soils and high biomass production capability with minimal inputs (McLaughlin *et al.*, 1999). A portion of the developmental effort with switchgrass as an HEC involves the breeding of cultivars with adaptations for specific environments and enhanced biomass yield capability. One of the breeding programmes involved in the collaborative research effort is located at the Oklahoma State University. Recurrent Selection for General Combining Ability (RSGCA) for increased biomass production is currently underway in one genetically broad-based population of lowland ecotype switchgrass, Southern Lowland 93 (SL-93), and two upland ecotype switchgrass populations, Southern Upland Northern Upland Early Maturing (SNU-EM) and Southern Upland Northern Upland Late Maturing (SNU-LM) (Oklahoma State University).

The breeding method commonly used to improve quantitatively inherited traits (such as biomass yield) in populations of outcrossing species such as switchgrass is RSGCA (Poehlman & Sleper, 1995). RSGCA can be employed most expeditiously to further selection when space-planted populations are assayed for the trait(s) of interest. Hopkins (2005) noted that, because of limited availability of seed for many applications in breeding programmes, the breeder is generally faced with the choice of either producing additional seed prior to evaluation in seeded sward plots or transplanting seedlings from randomly selected plants via a space-planted arrangement. Moreover, Vogel & Moore (1993) surmised that variability is difficult to observe under pasture or rangeland conditions and that seed harvested from individual plants and planted in uniformly space-planted nurseries would allow the elucidation of total genetic, additive and phenotypic variation within a given population. Humphreys (1989) reported that water-soluble carbohydrate concentration, dry matter (dm) digestibility and forage yield in perennial ryegrass (*Lolium perenne* L.) have shown similar responses in seeded sward plots and space-planted arrangements. Likewise, Burton (1974, 1982) reported that selection of spaced plants was effective in improving yield of Pensacola bahiagrass (*Paspalum notatum* var. *saure* Parodi) when evaluated in both space-planted and seeded sward plots.

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Increased biomass yield is an important breeding objective for switchgrass, but information concerning the magnitude of genetic variation for this trait is limited. Newell & Eberhart (1961) reported a broad-sense heritability (h^2_b) estimate of 0.78 for plant dm yield for forage production in a Nebraska upland switchgrass population. Newell & Eberhart (1961) also reported narrow-sense heritability (h^2_n) estimates for dm yield for forage of 0.18, 0.52 and 0.05 for 'small blue-green', 'medium-tall blue-green' and 'tall-green' plant populations derived from Nebraska and Kansas germplasm. Talbert *et al.* (1983) reported estimates of genetic parameters in a population of lowland switchgrass for *in vitro* dm disappearance, percent N dry weight and dry weight. They reported h^2_n estimates of 0.25 and 0.59 for dry weight on an individual plant and family basis, respectively. Van Esbroeck *et al.* (1998) calculated realised heritability estimates of 1.0 and 0.92 for early and late panicle emergence, respectively, in 'Alamo' switchgrass; the assumption being that late panicle emergence could be used to increase above-ground biomass yield. Boe & Lee (2007) reported h^2_n estimates of 0.60 and 0.62 from variance component methods for biomass yield for the upland ecotype varieties of switchgrass Sunburst and Summer, respectively. Das *et al.* (2004) reported significant variability for biomass yield and several yield components in switchgrass but did not report heritability estimates of these traits.

Estimates of heritable genetic variation and gains from selection within breeding populations are helpful to breeders in determining the probable effectiveness of pursuing the breeding process over time. Accordingly, the objectives of this study were to estimate h^2_n and ΔG for biomass yield within the SL-93 population of lowland switchgrass and the SNU-EM and SNU-LM populations of upland switchgrass.

Materials and methods

Plant materials consisted of half-sib (HS) families and clonal parental plants from one lowland switchgrass population (SL-93) and two upland switchgrass populations (SNU-EM and SNU-LM).

Southern Lowland 93 population

The SL-93 base population was synthesised in 1993 from plants of the variety 'Alamo' and the breeding population 'PMT-279'. The population providing plant materials for this study resulted from two cycles of restricted recurrent phenotypic selection for higher biomass yield as described by Burton (1982). In the spring 2001, 130 randomly selected HS families from a 1020 plant SL-93 selection nursery were planted in a randomised complete block design (RCBD) at the Perkins Research Station (35.57°N, 97.01°W) to assess biomass yield performance. Seeds from the randomly selected plants were grown in a greenhouse and were transplanted on 1.06-m centres in a field trial. A row of switchgrass plants, not harvested for biomass yield, was transplanted around the perimeter of the trial in order to guard against border effects. Individual plots consisted of three HS progeny plants. The soil type was a Teller loam (fine, loamy, mixed, active, thermic Udic Argiustolls).

So that unbiased estimates of h^2_n could be obtained (Casler, 1982) via progeny–parent regression, a replicated trial consisting of clonal parents of the HS families were planted in the spring 2002 on the Agronomy Research Station, Stillwater, OK (36.16°N, 97.09°W). Greenhouse-grown clonal plants were transplanted on 1.06-m centres in an RCBD (randomised complete block design) with three replications. A row of plants, not harvested for biomass yield, was established around the perimeter of the trial in order to prevent border effects. Individual plots consisted of one clonal parent plant. Asay *et al.* (2001) indicated that fewer parental plants per plot than progeny plants per plot may be used in progeny–parent regression studies because of identical genotypes of parental clones. The soil type was a Kirkland silt loam (fine, mixed, superactive, thermic Udertic Paleustolls).

Southern Upland Northern Upland populations

The two populations, SNU-EM and SNU-LM, were synthesised, respectively, from late-maturing and early-maturing plants from two populations designated 'Southern Upland' (SU) and 'Northern Upland' (NU) and from Oklahoma switchgrass accessions SWG001, SWG006 and SWG068. The original SU population was synthesised in 1993 from 'Caddo' and 'Blackwell'. Switchgrass accessions SWG001, SWG006 and SWG068 were subsequently merged into the SU population. The original NU population was synthesised in 1993 from 'Nebraska 28', 'Pathfinder' and 'Cave-in-Rock'. In 1998, isolated polycross nurseries were planted to form two populations designated as SNU-EM and SNU-LM. A total of 56 clonal parent plants, selected for flowering date compatibility, from the SU and NU populations were included in each polycross. Seed (C_0) was harvested from each polycross nursery in 1999. In 2000, 1020 C_0 plants of each population were space planted (1.06 m) for purposes of selection and estimating genetic variation within the populations. For this study, HS seed was harvested from 130 randomly selected plants from each nursery in the fall of 2001.

In spring 2002, 100 HS C_0 families from each population were established in an RCBD with four replications at the Perkins Research Station, Perkins, OK (35.57°N,

97.01°W) using plants started in the greenhouse. Greenhouse-grown plants were transplanted on 1.06-m centres. A row of plants, not harvested for biomass yield data, was established around the respective tests to protect against border effects. The soil type for both tests was a Teller loam (fine-loamy, mixed, active, thermic Udic Argiustolls).

So that unbiased estimates of h_n^2 could be obtained via progeny–parent regression methods (Casler, 1982), clonal parent plants of each HS progeny family from the SNU-EM and SNU-LM populations were established in an RCBD with three replications in spring 2002 at the Agronomy Research Station, Stillwater, OK (36.16°N, 97.09°W). Greenhouse-grown clonal plants of each parent were transplanted, one plant per plot, on 1.06-m centres. A row of plants, not harvested for biomass yield data, was established around the perimeter of the respective tests to protect against border effects. The soil corresponding to the two tests was a Kirkland silt loam (fine, mixed, superactive, thermic Udertic Paleustolls).

Cultural practices

All tests were fertilised annually in early spring with 90 kg ha^{-1} N. P and K were applied to all trials in early spring of each year as indicated by soil test results. Surflan® herbicide was applied to the tests early each spring at a rate of 2.24 kg ha^{-1} a.i. for the SL-93 population and at a rate of 1.70 kg ha^{-1} a.i. for the SNU-EM and SNU-LM populations to prevent switchgrass seedling emergence and to control other weeds. Individual plants of the SL-93 HS progeny trial were harvested in the fall of 2002 and 2003, and the corresponding clonal parental test was harvested in the fall of 2003 and 2004. Both trials were harvested prior to plant senescence. Individual plants of the SNU-EM and SNU-LM HS progeny trial were harvested in the fall of 2003 and 2004, prior to plant senescence. Likewise, the SNU-EM and SNU-LM clonal parent tests were harvested in the fall of 2003 and 2004, prior to plant senescence. Biomass samples were dried for approximately 1 week to determine dm concentration and convert total wet plant weights to dry weights.

Statistical procedures

For all populations, the data were analysed using generalised least squares (method = restricted maximum likelihood; SAS Institute, 1999). Statistical analyses of the populations were conducted on a whole experiment basis (over years) and within each year (2002 and 2003 for the SL-93 population, and 2003 and 2004 for the SNU populations). A two-factor analysis of variance was conducted on all data for all populations collected over all environments and years employing the following statistical effects model:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + \tau_k + \beta\tau_{jk} + e$$

where μ indicates overall mean of biomass yield; α_i, random effect of replication i; β_j, random effect of plant family (genotype) j; τ_k, fixed effect of year k; $\beta\tau_{jk}$, random interaction effect of plant family j and year k and e, experimental error, mean 0, variance σ^2.

For all populations, estimation of h_n^2 was conducted by progeny–parent regression via generalised least squares (method = type 3; SAS Institute, 1999).

Estimates of h_n^2 were calculated as follows:

$$2 \times \beta_1$$

where β_1 is the linear regression coefficient of progeny–parent regression.

The regression coefficient is derived as described and presented by Casler (1982) as follows:

$$h_n^2 = 2\frac{\sigma_{Ppo}}{\sigma_P^2}$$

where σ_{Ppo} is the phenotypic covariance between parental values and progeny values and σ_P^2, the phenotypic variance among parents.

Estimates of h_n^2 were calculated in this manner on both an individual plant and phenotypic family mean (PFM) basis.

Parent–offspring regression is a commonly used technique for estimating h_n^2 of quantitative characters in crop species (Casler, 1982). This technique, however, may lead to biased estimates of h_n^2 as a result of genotype × environment (GE) interactions and error covariances between parents and offspring. Furthermore, if these covariances are positive, the resulting positive bias to h_n^2 will result in overly optimistic expected genetic advances (Casler, 1982). To compensate for that error, progeny plot mean and progeny individual plant biomass yield were regressed onto parent means, averaged across replications, from a separate environment and year. Levings & Dudley (1963) concluded that the best estimate of h_n^2 in autotetraploids and in diploids probably results from doubling the regression coefficient from offspring on parent.

ΔG per cycle of selection was also calculated on both an individual plant and PFM basis as described by Nguyen & Sleper (1983).

ΔG per cycle of selection can be predicted as follows:

$$\Delta G = ckh_n^2\sigma_P = ck2\frac{\sigma_{PO}}{\sigma_P^2}$$

where c is parental control factor; k, standardised selection differential; h_n^2, narrow-sense heritability; σ_P,

phenotypic standard deviation from clonal parent plants; σ_{PO}, covariance between parent and HS families or individual plants and σ_P^2, phenotypic variance of clonal plant families.

Here, $c = 2$ and $k = 1.16$.

Results

Southern Lowland 93 population

Highly significant variation ($P < 0.01$) was detected among HS families of the SL-93 population for dry biomass yield within years (2002–2003) (data not presented) and over years (Table 1). The biomass yield of the HS families ranged from 0.83 to 1.67 kg dm plant^{-1}. In the combined analysis, the fixed main effect of years was highly significant ($P < 0.01$). The year × family interaction effect was not significant ($P < 0.05$). The variance components of HS progeny and parent plants (Table 1) (σ_F^2) were relatively small but significantly greater than 0. The family × year (σ_{FY}^2) component was 0, indicating lack of GE interaction. HS families ranked similarly between 2002 and 2003 for biomass yields based on a Spearman's rank correlation coefficient of $r_S = 0.77$ ($P < 0.01$). Furthermore, the raw ranks of the families within each year of the study were examined. Based on a 30% selection intensity, 39 parent plants would be selected based on their HS family performance. Twenty-seven of the highest yielding 39 parent plants were found to be in common for both years of the study.

Significant genetic variation was found for biomass yield in the SL-93 clonal parental switchgrass population via the σ_F^2 component in analyses for the years 2003 and 2004 as well as in the analysis over both years of the study. In the combined analysis, significant GE interaction (σ_{FY}^2) was detected ($P < 0.05$) (Table 1).

For the SL-93 population, estimates of h_n^2 were 0.12 and 0.13 based on PFM and individual plant selection, respectively. Corresponding ΔG values per selection cycle were low, 0.15 kg dm plant^{-1} and 0.10 kg dm plant^{-1} for PFM and individual plant selection, respectively (Table 2).

Table 1 Estimates of variance components and their associated standard errors for the SL-93 switchgrass HS families evaluated for biomass yield at Perkins, OK, 2002–2003, and SL-93 clonal parents evaluated for biomass yield at Stillwater, OK, 2003–2004

	Population	
Variance Component	SL-93 HS Progeny	SL-93 Clonal Parents
Family (σ_F^2)	0.1033** ± 0.0150	0.2134** ± 0.0340
Family × year (σ_{FY}^2)	0 ± —	0.0238* ± 0.0150
Residual (σ_e^2)	0.3046 ± 0.0155	0.2687 ± 0.0165

HS, half-sib; SL-93, Southern Lowland 93.
* and ** indicate significance at the 0.05 and 0.01 probability levels, respectively.

Southern Upland Northern Upland populations

In both the SNU-EM and the SNU-LM populations, analysis of variance of HS family biomass yields over years indicated highly significant differences ($P < 0.01$) because of years and the family × year interaction but not families ($P < 0.05$) (Tables 3 and 4). Yield differences among HS families in both populations were highly significantly different ($P < 0.01$) for each of the 2 years (data not presented). Biomass yield of the SNU-EM population ranged from 0.38 to 0.80 kg dm plant^{-1}, and for the SNU-LM population, the mean biomass yield of HS families ranged from 0.49 to 1.02 kg dm plant^{-1}. The Spearman's rank correlation coefficients for the SNU-EM and SNU-LM populations were $r_S = 0.06$ ($P > 0.05$) and 0.05 ($P > 0.05$), respectively, indicating that the HS family rankings for biomass yield were not similar for 2003 and 2004 for either population.

In both populations, yield differences among parent plants were significantly different within and over years. Estimates of variance components for biomass yield were calculated for HS progeny families and clonal parents of the SNU-EM and SNU-LM populations (Tables 3 and 4). Although estimates of σ_F^2 for HS progeny were small in both populations and were not significant ($P > 0.05$) as determined by an F-test, σ_F^2 for clonal parents and the σ_{FY}^2 estimates for HS families and clonal parents were highly significant ($P < 0.01$). The results also indicated that differential genotypic yield response to environment (year) was large and that testing over years is required to evaluate switchgrass genotypes for quantity and stability of biomass yield.

Estimates of h_n^2 from progeny–parent regression for individual plants were of similar magnitude for the two populations (0.44 and 0.47 for SNU-EM and SNU-LM, respectively). The individual plant versus PFM h_n^2 estimates were nearly identical (Table 2). Predicted yield gains per selection cycle ranged from 0.22 to 0.33 kg dm plant^{-1} (Table 2).

Discussion

Estimates of heritable genetic variation and ΔG within breeding populations are helpful to breeders in determining the probable effectiveness of pursuing selection strategies over time. For the SL-93 population, estimates of h_n^2 (0.12 and 0.13 for PFM and individual plant selection, respectively) obtained from the progeny–parent regression method were considerably lower for both PFM and individual plant selection than those reported

Table 2 Narrow-sense heritability estimates (h_n^2) for biomass yield, 95% confidence intervals (CIs) of those h_n^2 estimates, and predicted genetic gains (ΔG) per cycle of selection (5 years per cycle) and per year for the SL-93, SNU-EM, and SNU-LM populations based on progeny–parent regression techniques for PFMs and for individual plant selection

Population	h_n^2 Estimate	95% CI	ΔG Selection Cycle (kg dm plant^{-1})	% ΔG Year (kg dm plant^{-1})
SL-93 – PFM	0.12	(−0.05, 0.30)	0.15	0.03
SL-93 – individual plant	0.13	(−0.04, 0.30)	0.10	0.02
SNU-EM – PFM	0.45	(0.30, 0.59)	0.22	0.04
SNU-EM – individual plant	0.44	(0.30, 0.59)	0.27	0.05
SNU-LM – PFM	0.46	(0.30, 0.63)	0.22	0.05
SNU-LM – individual plant	0.47	(0.31, 0.63)	0.33	0.07

PFM, phenotypic family mean; SL-93, Southern Lowland 93; SNU-EM, Southern Upland Northern Upland Early Maturing; SNU-LM, Southern Upland Northern Upland Late Maturing.

by Talbert *et al.* (1983) in a lowland switchgrass population via estimation from variance component methods (0.59 and 0.25 for PFM and individual plant selection, respectively). This may be, in part, due to the progeny–parent regression method employed in elucidating estimates of h_n^2 for the populations in this study, which tends to produce conservative estimates of h_n^2 (Casler, 1982). Although the 95% confidence intervals (CIs) for both PFM and individual plant selection h_n^2 estimates obtained from progeny–parent regression techniques are inclusive of 0, it is important to note that the CIs for both estimates are extremely wide. Although values of ΔG for both PFM and individual plant selection in the SL-93 population were low, the results suggest that the magnitude of additive genetic variance for biomass yield within the SL-93 population is sufficient to provide positive response to selection based on HS PFM individual plant performance.

The relatively higher estimates of h_n^2 within the SNU-EM and SNU-LM populations (ranging from 0.45 to 0.47 for PFM and individual plant selection considered jointly) also suggest ample additive genetic variance for positive response to selection for biomass yield. Although these h_n^2 estimates are considerably lower than those reported by Boe & Lee (2007) for upland switchgrass varieties in which considerable selection has been practiced, they are markedly higher than those reported by Newell & Eberhart (1961) for small blue-green (0.18) and tall blue-green upland switchgrass populations (0.05) for dm forage yield.

The failure of HS families in both populations to respond similarly for biomass yield within different years of the study masked differences evident within individual years. Differences in weather patterns between the 2 years of the test may have contributed to the differences in ranking of the HS families. In order to quantify different weather patterns within the growing seasons of 2003 and 2004, data from the Oklahoma Mesonet (2007) were obtained. Daily high and average temperatures were highly significantly different between the years ($P < 0.001$) as determined by a Student's *t*-test for the months of July, August and September. The range of average daily temperatures was from 12.27°C to 34.17°C and from 18.94°C to 30.50°C for 2003 and 2004, respectively. Precipitation for the period totalled 202.40 cm for 2003 and 163.60 cm for 2004. The significant year × HS progeny interactions for the SNU-EM and SNU-LM populations, which may be the result of these weather patterns, clearly indicate the need for multiyear evaluations of HS families.

Table 3 Estimates of variance components and their associated standard errors for the SNU-EM HS progeny and clonal parental populations tested at Perkins and Stillwater, OK, respectively, 2003–2004

	Population	
Variance Component	SNU-EM HS Progeny	SNU-EM Clonal Parents
Family (σ_F^2)	0.0006 ± 0.0016	0.0359** ± 0.0064
Family × year (σ_{FY}^2)	0.098** ± 0.0022	0.0084** ± 0.0024
Residual (σ_e^2)	0.0228 ± 0.0013	0.02463 ± 0.0018

HS, half-sib; SNU-EM, Southern Upland Northern Upland Early Maturing.
** indicates significance at the 0.05 and 0.01 probability levels, respectively.

Table 4 Estimates of variance components and their associated standard errors for the SNU-LM HS progeny and clonal parental populations tested at Perkins and Stillwater, OK, respectively, 2003–2004

	Population	
Variance Component	SNU-LM HS Progeny	SNU-LM Clonal Parents
Family (σ_F^2)	0.0013 ± 0.0024	0.0325** ± 0.0065
Family × year (σ_{FY}^2)	0.0144** ± 0.0032	0.0060* ± 0.0035
Residual (σ_e^2)	0.0337 ± 0.0020	0.0507 ± 0.0036

HS, half-sib; SNU-LM, Southern Upland Northern Upland Late Maturing.
* and ** indicate significance at the 0.05 and 0.01 probability levels, respectively.

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References

Asay K.H., Mayland H.F., Jefferson P.G., Berdahl J.D., Karn J.F., Waldron B.L. (2001) Parent-progeny relationships and genotype × environment effects for factors associated with grass tetany and forage quality in Russian wildrye. *Crop Science*, **41**, 1478–1484.

Boe A., Lee D.K. (2007) Genetic variation for biomass production in prairie cordgrass and switchgrass. *Crop Science*, **47**, 929–934.

Burton G.W. (1974) Recurrent restricted phenotypic selection increases forage yields of Pensacola bahiagrass. *Crop Science*, **22**, 831–835.

Burton G.W. (1982) Improved recurrent restricted phenotypic selection increases bahiagrass forage yields. *Crop Science*, **22**, 1058–1061.

Casler M.D. (1982) Genotype × environment interaction bias to parent–offspring regression heritability estimates. *Crop Science*, **22**, 540–542.

Das M.K., Fuentes R.G., Taliaferro C.M. (2004) Genetic variability and trait relationship in switchgrass. *Crop Science*, **44**, 443–448.

Henry D.S., Taylor T.H. (1989) Registration of KY 1625 switchgrass germplasm. *Crop Science*, **29**, 1096.

Hopkins A.A. (2005) Grazing tolerance of cool-season grasses planted as seeded sward plots and spaced plants. *Crop Science*, **45**, 1559–1564.

Hopkins A.A., Vogel K.P., Moore K.J., Johnson K.D., Carlson I.T. (1995) Genotypic variability and genotype × environment interactions among switchgrass accessions from the Midwestern USA. *Crop Science*, **35**, 565–571.

Hopkins A.A., Taliaferro C.M., Murphy C.D., Christian D. (1996) Chromosome number and nuclear DNA content of several switchgrass populations. *Crop Science*, **36**, 1192–1195.

Humphreys M.O. (1989) Water-soluble carbohydrates in perennial ryegrass breeding III. Relationships with herbage production, digestibility, and crude protein content. *Grass and Forage Science*, **44**, 423–430.

Levings C.S., Dudley J.W. (1963) Evaluation of certain mating designs for estimation of genetic variance in autotetraploid alfalfa. *Crop Science*, **9**, 58–61.

Martinèz-Reyna J.M., Vogel K.P. (2002) Incompatibility systems in switchgrass. *Crop Science*, **42**, 1800–1805.

Martinèz-Reyna J.M., Vogel K.P., Caha C., Lee D.J. (2001) Meiotic stability, chloroplast DNA polymorphisms, and morphological traits of upland × lowland switchgrass reciprocal hybrids. *Crop Science*, **41**, 1579–1583.

McLaughlin S., Bouton J., Bransby D., Conger B., Ocumpaugh W., Parrish P., Taliaferro C., Vogel K., Wullschleger S. (1999) Developing switchgrass as a bioenergy crop. In *Perspectives on New Crops and Uses*, pp. 282–299. Ed. J. Janick. Alexandria, VA, USA: ASHA Press.

Moser L.E., Vogel K.P. (1995) Switchgrass, big bluestem and indiangrass. In *Forages Vol. 1, An Introduction to Grassland Agriculture*. 5th edn. pp. 409–420. Ed. Michael Collins. Ames, IA, USA: Iowa State University Press.

Newell L.C., Eberhart S.A. (1961) Clone and progeny evaluation in the improvement of switchgrass, *Panicum virgatum* L. *Crop Science*, **1**, 117–121.

Nielson E.L. (1944) An on-farm test of perennial forage grass varieties under management intensive grazing. *Journal of Agronomy Research*, **69**, 327–353.

Nguyen H.T., Sleper D.A. (1983) Theory and application of half-sib matings in forage grass breeding. *Theoretical and Applied Genetics*, **64**, 187–196.

Oklahoma Mesonet. (2007) *Oklahoma Mesonet climatological summary data for Perkins, OK, USA* [WWW document URL]. http://www.mesonet.org/ (accessed on 22 January 2007).

Parrish D.J., Fike J.J. (2005) The biology and agronomy of switchgrass biofuels. *Critical Reviews in Plant Sciences*, **24**, 423–459.

Poehlman J.M., Sleper D.A. (1995) In *Breeding Field Crops*. 4th edn. pp.184–185. Ames, IA, USA: Iowa State University Press.

Porter C.L. Jr (1966) An analysis of variation between upland and lowland switchgrass, *Panicum virgatum* L., in central Oklahoma. *Ecology*, **47**, 980–992.

Sanderson M.A. (1992) Morphological development of switchgrass and kleingrass. *Agronomy Journal*, **84**, 415–419.

Sanderson M.A., Reed R.L., McLaughlin S.B., Wullschleger S.D., Conger B.V., Parrish D.J., Wolf D.D., Taliaferro C., Hopkins A.A., Ocumpaugh W.R., Hussey M.A., Read J.C., Tischler C.R. (1996) Switchgrass as a sustainable bioenergy crop. *Bioresource Technology*, **56**, 83–93.

Sanderson M.A., Read J.C., Reed R.L. (1999) Harvest management of switchgrass for biomass feedstock and forage production. *Agronomy Journal*, **91**, 5–10.

SAS Institute (1999) *SAS System for Windows. Version 8.2*. Cary, NC, USA: SAS Institute.

Talbert L.E., Timothy D.H., Burns J.C., Rawlings J.O., Moll R.H. (1983) Estimates of genetic parameters in switchgrass. *Crop Science*, **23**, 725–728.

Taliaferro C.M. (2002) *Breeding and selection of new switchgrass varieties for increased biomass production. Oak Ridge National Laboratory*. [WWW document]. URL http://www.ornl.gov/~Ewebworks/cppn/y2001/rpt/116285.pdf (accessed on 20 April 2005).

Van Esbroeck G.A., Hussey M.A., Sanderson M.A. (1998) Selection response and developmental bias for early and late panicle emergence in Alamo switchgrass. *Crop Science*, **38**, 342–346.

Vogel K.P., Moore K.J. (1993) Native North American grasses. In *New Crops*, pp. 284–293. Eds J. Janick and J.E. Simon. New York, NY, USA: Wiley.

Vogel K.P., Gorz H.J., Haskins F.A. (1989) *Breeding Grasses for the Future. Crop Science Society of America from Breeding Turf and Forage Grasses*. Madison, WI, USA: CSSA Special Publication 15.